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VESTIBULAR MECHANISMS AND VISION*

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VESTIBULAR MECHANISMS AND VISION

The purpose of this report is to summarize briefly the results of some investigations carried out at the U. S. Naval School of Aviation Medicine dealing with the vestibular and visual systems under the influence of unusual gravitational-inertial force environments (GIFE). The initial stimulus for these researches stemmed from the need to evaluate the role of the GIFE in causing disorientation in pilots, and now space flight has provided an added impetus. It was learned early that exposure to unusual force environments greatly affected the flyer through the sensory receptors in his vestibular organs and through them visual mechanisms and that, in turn, vision and the visual environment also affected the responses to stimulation of the vestibular organs. Thus, exposure to angular acceleration, the physiological stimulus to the semicircular canals, resulted in apparent movement of an object which was fixed in relation to the observer. This has been termed the oculogyral illusion, and its behavior bears a definite relation to the pattern of angular acceleration. Unusual patterns evoked bizarre effects. The Coriolis phenomenon may be regarded as a special instance of the oculogyral illusion in response to simultaneous rotation of the head about two axes which generates a Coriolis acceleration. Ocular nystagmus may be an associated response to angular and Coriolis accelerations and, when prominent, contributes to the illusion.

When a person is exposed to linear acceleration with a change in direction of the resultant force relative to himself, he not only feels that he is being tilted but he also perceives an apparent displacement of objects in the visual field which tend to accord with the new direction of the mass acceleration. The visual component has been termed the oculogravic illusion which has quite different characteristics from the oculogyral or Coriolis illusions. An associated phenomenon is ocular counterrolling which is manifested to a greater degree than when a person simply tilts with respect to the gravitational upright.

Simultaneous exposure to linear and angular acceleration alters the responses in a characteristic manner, suggesting a close functional relationship between the two vestibular organs. Positional nystagmus, and positional alcohol nystagmus may be dependent on this relationship.

In carrying out our experiments an attempt was made to simulate the unusual force environments in the laboratory, but in the case of weightlessness it was necessary to go aloft. It was relatively easy to control vision and the visual environment, and it was possible to control the inputs from the semicircular canals and the otolith apparatus by the use of subjects who had lost the function of the canals and, probably, also of the otoliths. Our investigations sought to exploit these vestibulo-visual phenomena 1) in testing the function of the semicircular canals and the otolith organs, 2) in using these phenomena as indicators in the investigation of different psychophysiological mechanisms including adaptation, and 3) in attempting to show how these mechanisms are affected under the unusual force environments to which man may be subjected in an aircraft or space vehicle.

OTOLITH ORGANS AND VISION

Linear acceleration, considered the adequate stimulus to the macular end organs, can be varied to evoke changes in overt behavior by repositioning the head (actually the otolith organs themselves) with respect to gravity, moving it in a circular path at a constant rate, or in a rectilinear path at an accelerating rate. Direction of the stimulus force is controlled by orienting the head with respect to the resultant gravitational-inertial force, which varies in magnitude as a function of velocity. Normal gravitational acceleration can be counteracted completely or partially within the earth's gravitational field by Keplerian trajectory flight maneuvers. The otolith organs of humans can be probed remotely by linear acceleration in a way analogous to the direct mechanical stimulation of these organs in animals. It is possible to apply forces of various magnitude in specific directions relative to the anatomical spatial arrangement of the otolith organs within the skull; the mode of action and role in perception of the otolith organs can then be determined indirectly by measuring external changes such as occur in ocular counterrolling and egocentric visual localization. Subjects with known labyrinthine defects offer a means of evaluating the extent to which extra-labyrinthine factors are involved in these external signs of inner ear function.

1. Counterrolling

When certain experimental procedures are followed, the conjugate rolling movement of the eyes around their lines of sight opposite to the lateral inclination of the head is generally held to be a direct reflex originating in the otolith organ. The distinct advantage of having an external indicator of otolith activity which is not under voluntary control has been outweighed in the past by the great difficulty in obtaining precise measurements of the rolling movements. Throughout the long colorful history of counterrolling studies, several methods of measuration have been used (1). All have as a common basis the selection of anatomical landmarks on the eye to establish a reference plane containing the line of sight for specifying the rotation of the eye around its line of sight. The most accurate of these older methods yielded a measuring error which was large even in relation to the maximum amount of counterrolling, in some cases less than six degrees, that can be evoked by head inclination.

A method involving photography of natural landmarks on the iris was devised to meet the requirement of greater precision in measuration. A solution to the problem of measuring very samll amounts of movement of these landmarks was found in simple magnification. In this procedure the film image of the entire eye is enlarged over 300 times the actual eye size by projection onto a distant screen. Measurement of angular torsional movement around the center of the pupil is then accomplished by superimposing upon each test image in succession, a second projected image of the subject's eye serving as a standard of comparison. More complete details of this measuring technique have been published (1). It is sufficient for this discussion to point out that a high degree of accuracy and reliability in measuration ($\simeq \pm 5$ minutes of arc) is possible with this procedure.

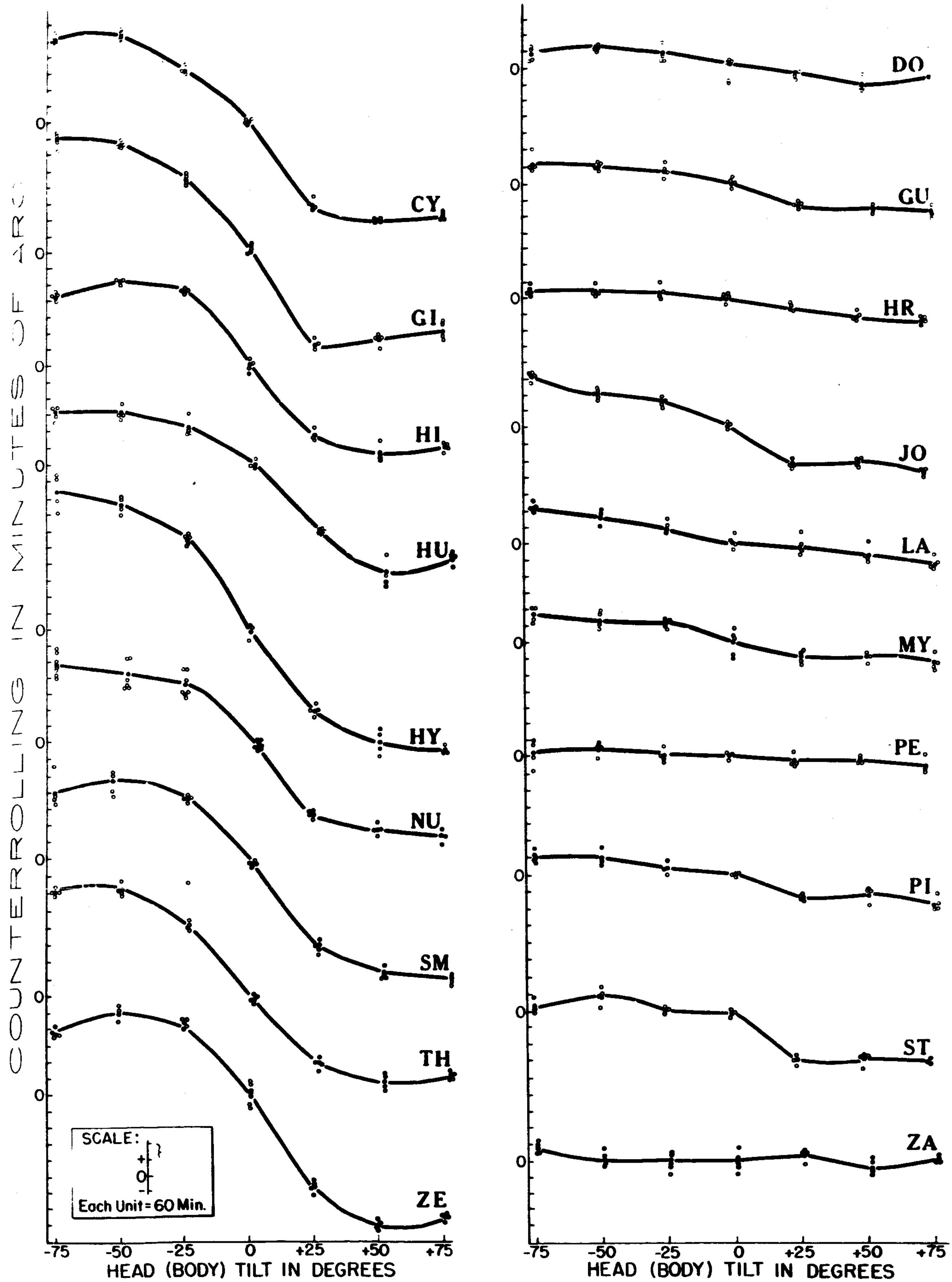
a. Normal Subjects

Counterrolling measurements using the photographic technique have been made on several normal individuals tilted in 25 degree steps up to $\pm 75^{\circ}$ from the gravitational vertical (2). Each of these subjects revealed a qualitatively similar counterrolling response (Figure 1) to head inclination but quantitatively there were interindividual differences. There were also significant right-left differences in some individuals but not in others. A more extensive study (1) was also conducted in which measurements were made at every 15 degrees within the frontal, sagittal, and two intermediate planes. Maximal compensatory torsional eye movement was found in the frontal plane, somewhat less in the intermediate planes, and not at all in the sagittal plane.

The absence of appreciable counterrolling when the head is tilted in its sagittal plane does not justify any inference that compensatory eye reflexes

Figure 1

Mean Counterrolling Values Plotted as a Function of Leftward and Rightward Tilt (Left Column: Normals, Right Column: L-D Subjects, Closed Circles Average Values in Minutes of Arc, Open Circles: Values for Different Trials at a Given Body Position). (Miller and Graybiel, *Ann. Otol., etc., St. Louis*)


COUNTERROLLING IN MINUTES OF ARC
CY
GI
HI
HU
HY
NU
SM
TH
ZE
DO
GU
HR
JO
LA
MY
PE
PI
ST
ZA
SCALE:
Each Unit = 60 Min.
-75 -50 -25 0 +25 +50 +75
HEAD (BODY) TILT IN DEGREES
-75 -50 -25 0 +25 +50 +75
HEAD (BODY) TILT IN DEGREES

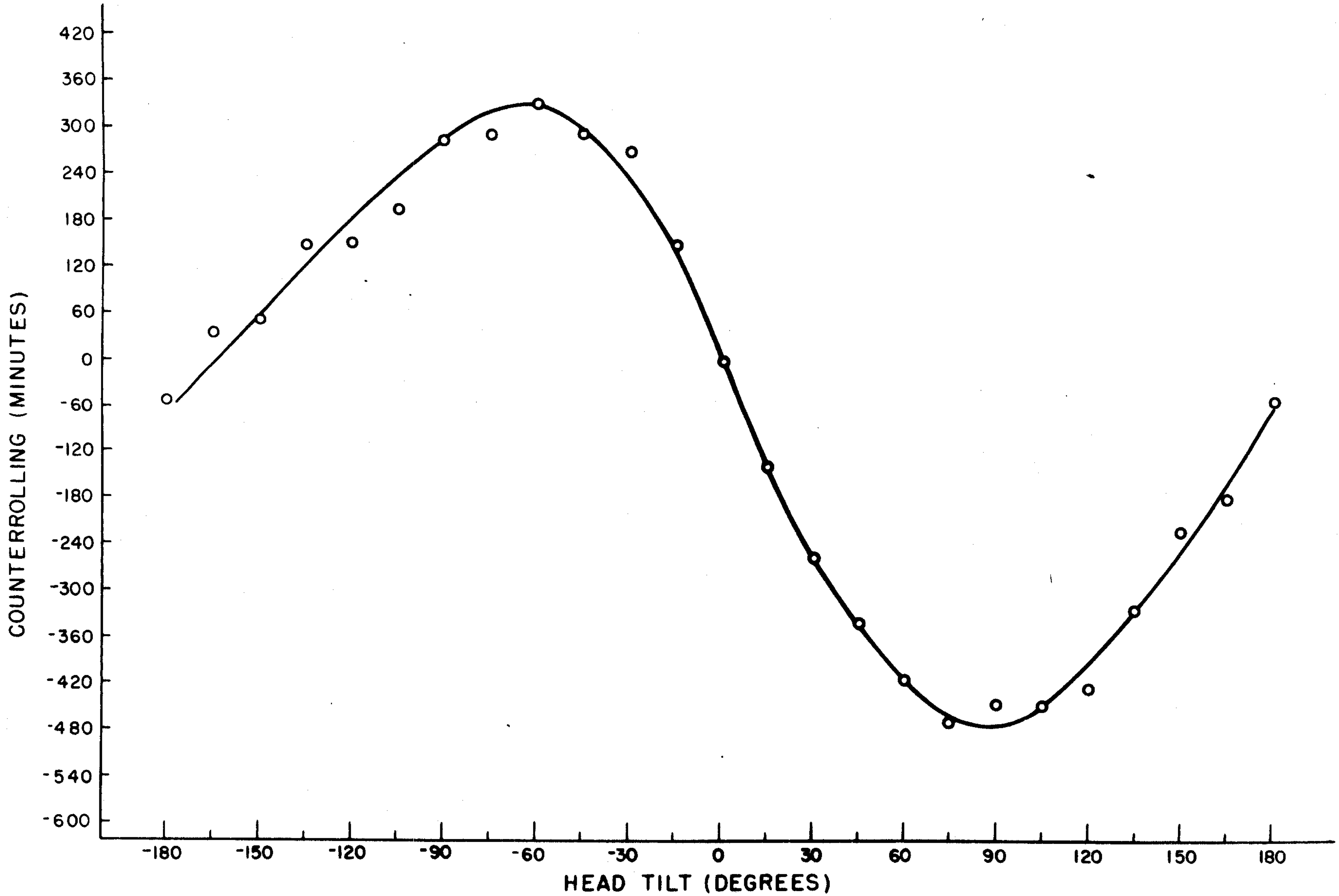
arising in the otolith organs do not exist when tilting in this plane. On the contrary, there is evidence that the eyes move reflexly in a vertical direction directly counter to the fore-and-aft tilting of the head. In the counter-rolling experiments innervations to elevate or depress the eyes was compensated by counter-fixational innervation. Counterrolling was always found to occur (Figure 2) opposite to the lateral component of head tilt and to increase fairly rapidly up to maximum at a head inclination between 60° and 90°. From this point on counterrolling decreased, but at a lesser rate than it increased, reaching about zero when the head was positioned vertically downward. The curve in Figure 2 represents the average of several values obtained at each position for each head position. A considerable amount of variability among individual measurements far greater than the measuring error has been found in almost every subject tested, indicating that a certain amount of physiological unrest also exists with respect to the antero-posterior axis of the eye. This variability has been observed by several authors using various measuring techniques.

By the use of counterrolling and known anatomical data a theory ("inward shearing") was developed in an attempt to explain the mechanism of otolith stimulation. It was proposed that each of the otolith organs (utricles and saccules) can be stimulated physiologically only by a shearing force applied inwardly, i.e., toward the median sagittal plane. This unidirectional response, furthermore, reaches its maximum when the direction of

Figure 2

Counterrolling (Average Values) as a Function of Lateral Head Tilt.

(Miller, _Acta_ _Otolaryng._ _Stockh._)


COUNTERROLLING (MINUTES)
420
360
300
240
180
120
60
0
-60
-120
-180
-240
-300
-360
-420
-480
-540
-600
-180
-150
-120
-90
-60
-30
0
30
60
90
120
150
180
HEAD TILT (DEGREES)

8

the force (gravity) is parallel to the individual macular planes. In its active zone the response of each otolith as indicated by counterrolling movements appears to vary as a cosine square function of the angular displacement of the inward direction of the macula from the force of gravity. If the response were proportional to the gravity component in the inward direction of the macula, then the response would be proportional to cosine of this displacement. But this simple relationship did not conform to the findings. The structure of the otolith organ apparently is such as to dampen the effect of gravity in yielding the cosine square function. A more complete discussion of these factors has been presented elsewhere (1). An important aspect of the general theory is the assumption that the saccules like the utricles act as gravireceptors and when activated contribute a smaller, yet significant, effect upon counterrolling. There are several studies that would tend to support the supposition that the saccule functions as an equilibrial organ.

b. Labyrinthine-Defective Subjects

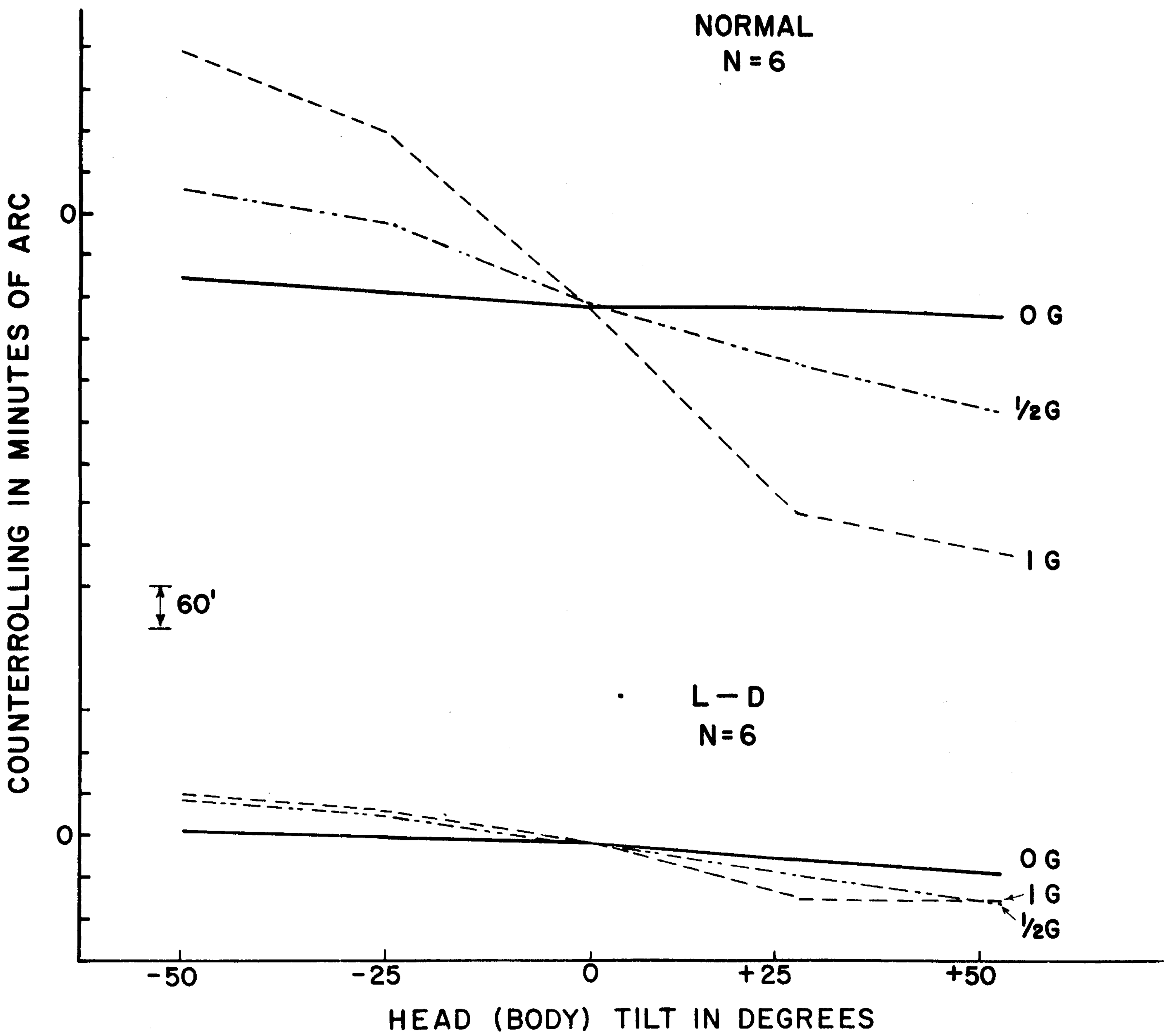
The photographic technique is particularly useful in measuring smaller than normal amounts of counterrolling that are found in individuals with disease-or otherwise-damaged vestibular organs. Investigators with less sensitive measuring devices had the difficult task of differentiating between a relatively large measuring error and a possible small residuum of otolith function. Information gained from precise measurements of otolith organ activity is needed to evaluate completely the inner ear organ triad and would complement the now routine audiometric and caloric irrigation tests of the other two auricular organs. If counterrolling, as has been assumed, is a specific indicator of otolith activity, then the level of function should be revealed in the character of the counterrolling response. In order to examine this theory, ten deaf subjects with bilateral loss of the semicircular canals were used as subjects for counterrolling measurements (2). As can be seen in Figure 1 these labyrinthine-defective (L-D) subjects did not disclose the characteristic pattern found in normal subjects in most instances. The magnitude of the response was in all cases less than in a comparable normal group. In some instances, there was no definite evidence of counterrolling, in others it was limited to one direction of tilt, and in still others there was a small but regular dependence of counterroll with the successive increase in bodily tilt. The highly significant differences between the normal and L-D groups must have been due to loss of function of the auricular sensory organs. More specifically, since there is no evidence that the counterrolling reflex is released by the organ of Corti, and insufficient evidence that it originates in the semicircular canals, but good evidence that it is released by the otoliths, it was concluded that the reduction in counterrolling in these cases was the result of injury to the otoliths. Interindividual differences in the L-D group are best explained by the presence of some residual otolith function. It was proposed that a single index (Counterrolling, CI) calculated as one half of the difference between the greatest maximum roll associated with leftward and rightward tilt be used to describe the functional status of the otolith organs for a given individual.

c. Effect of Change in Gravitational Inertial Force Environments

Counterrolling can also serve as an indicator of the effect of physiological deafferentation of the otolith organs brought about by eliminating or reducing the gravitational inertial force environment. The counterrolling response of six normal and six L-D subjects was measured at five different tilt positions under zero G, one-half G, and standard G conditions (3). The average results of the normal and L-D groups are portrayed in Figure 3. In the case of the normal subjects otolith activity as indicated by counterrolling response decreased in a regular fashion as the force was reduced. In the weightless condition tilting the normal individual would appear to have little effect upon the output of the otolith organs under the conditions of the test (3). The L-D subjects manifested a greatly reduced but similar pattern to the normals. This could be accounted for either as a residuum of otolith function in certain of the L-D subjects or as an effect of stimulation to extra-labyrinthine source(s) of tonic innervation to the extraocular muscles. The former explanation seems more reasonable based

Figure 3

Counterrolling as a Function of Magnitude of Gravitational Force (Zero G, 1/2 G, 1 G) and Head (Body) Position with Respect to Direction of Force in Normal and Labyrinthine Defective (L-D) Subjects.


NORMAL
N = 6
L — D
N = 6
0 G
½ G
1 G
0 G
1 G
½ G
60'
0
0
-50
-25
0
+25
+50
HEAD (BODY) TILT IN DEGREES
COUNTERROLLING IN MINUTES OF ARC

upon the results of the oculogravic illusion test and the care exercised to eliminate cervical, fixational, or binocular sources of cyclorotational eye movement. Even if these factors were involved, their importance is not great, as evidenced by the small maximum amount of counterrolling in the L-D group; thus it seems more reasonable to assume that otolith function has been revealed. It is interesting to note that, in the normal group of subjects, the one-half G curve falls somewhat short of the midway points between zero and one G as might be predicted. The significance of this finding is not known.

Information concerning the effect upon otolith activity (counterrolling) of increased gravitational-inertial force is provided by another study (4). As shown in Figure 4 the counterroll varies as a function of the magnitude of the lateral force even beyond the standard level of one G. This demonstrates the important fact that the counterrolling response is normally stimulus bound and its limit is not reached even with a lateral force of 2.25 G. The function at this higher level, however, is no longer linear.

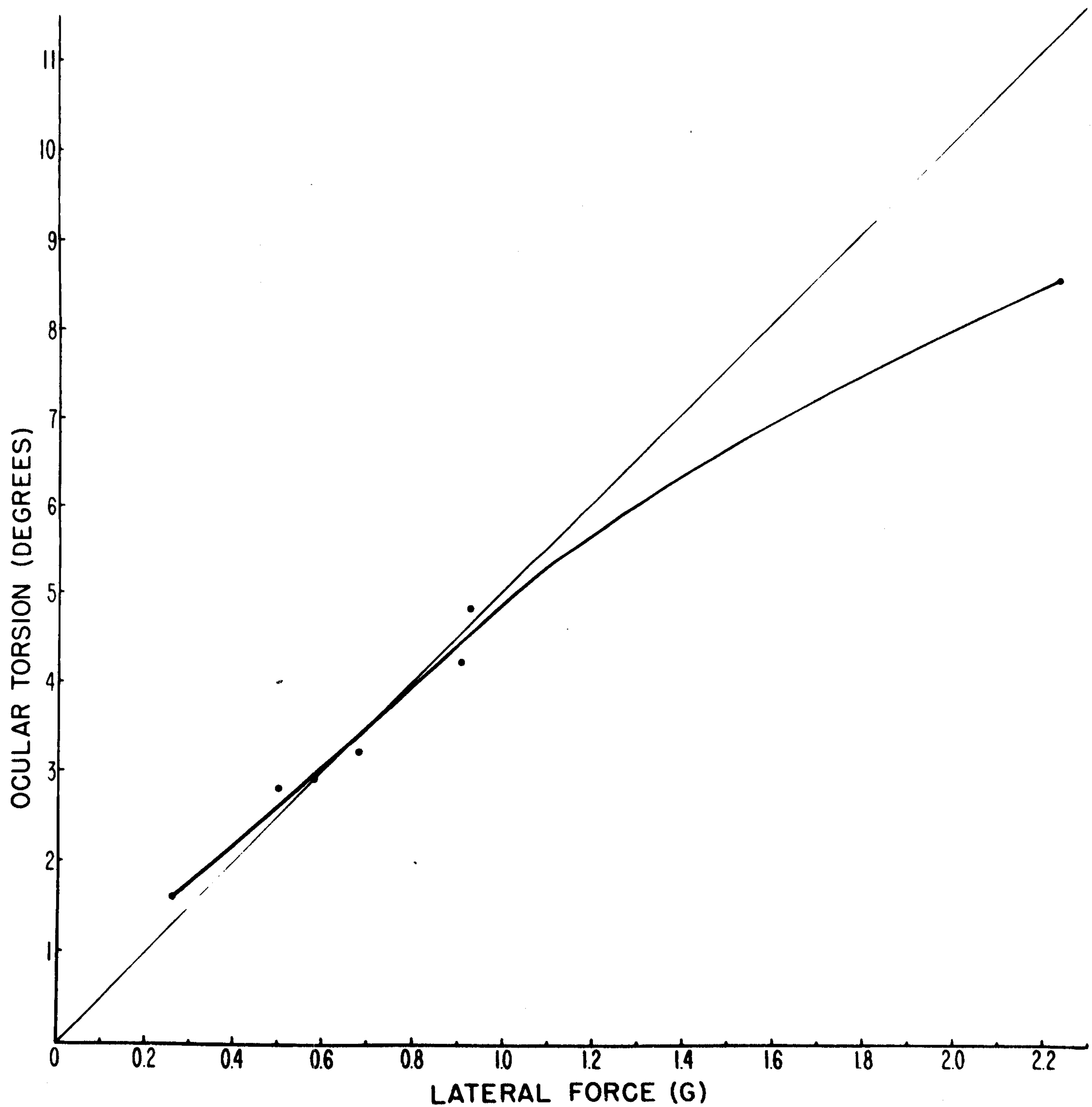
II. Egocentric Visual Localization

a. Aubert's Phenomenon and Its Variants

Man's absolute localization of objects in space is made with respect to his egocentric frame of reference. This frame of reference in

Figure 4

Degree of Counterroll as a Function of Magnitude of Force Acting Laterally on the Body (Head). (Woellner and Graybiel, J. Appl. Physiol.)



OCULAR TORSION (DEGREES)
LATERAL FORCE (G)
0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
1.8
2.0
2.2
1
2
3
4
5
6
7
8
9
10
11

turn is influenced by the action and interaction of certain body mechanisms providing visual, vestibular, tactual, proprioceptive, and other cues. When adequate visual cues are visible, these normally dominate all others so that judgments of the principal axes of space are quite precise, stable, and easily rendered (5). Removal of empirical visual cues, on the other hand, reveals considerable errors in perception, plus loss of stability and ease in localization, especially when the direction of the gravitational (inertial) force deviates appreciably from the longitudinal axis of the head (body). In the upright position, judgment of horizontality in normal individuals is not appreciably affected by the removal of visual cues. When individuals are placed in a recumbent position, however, and background cues are removed suddenly they observe, after a brief lag period, a gradual spontaneous rotation of the phenomenal horizontal up to a maximum displacement typical for a given individual. Superimposed upon these changes is the fluctuant movement of the apparent horizontal (rotary autokinesis) (5). The time course of these illusions in four subjects is presented in Figure 5.

In addition to these relatively small fluctuations about the considerable average deviation, the average level of deviation itself was found (6) to vary from test period to test period as illustrated in Figure 6 (heavy lines represent average of the several daily curves [thin lines]).

Figure 5

Time Course of Perception of Horizontality for Each of Four Subjects in Upright (Broken Line) or Recumbent (Continuous Line) Posture With (Unshaded Strips) and Without (Shaded Strips) Visual Reference Cues. (Miller and Graybiel, _Aerospace Med._)

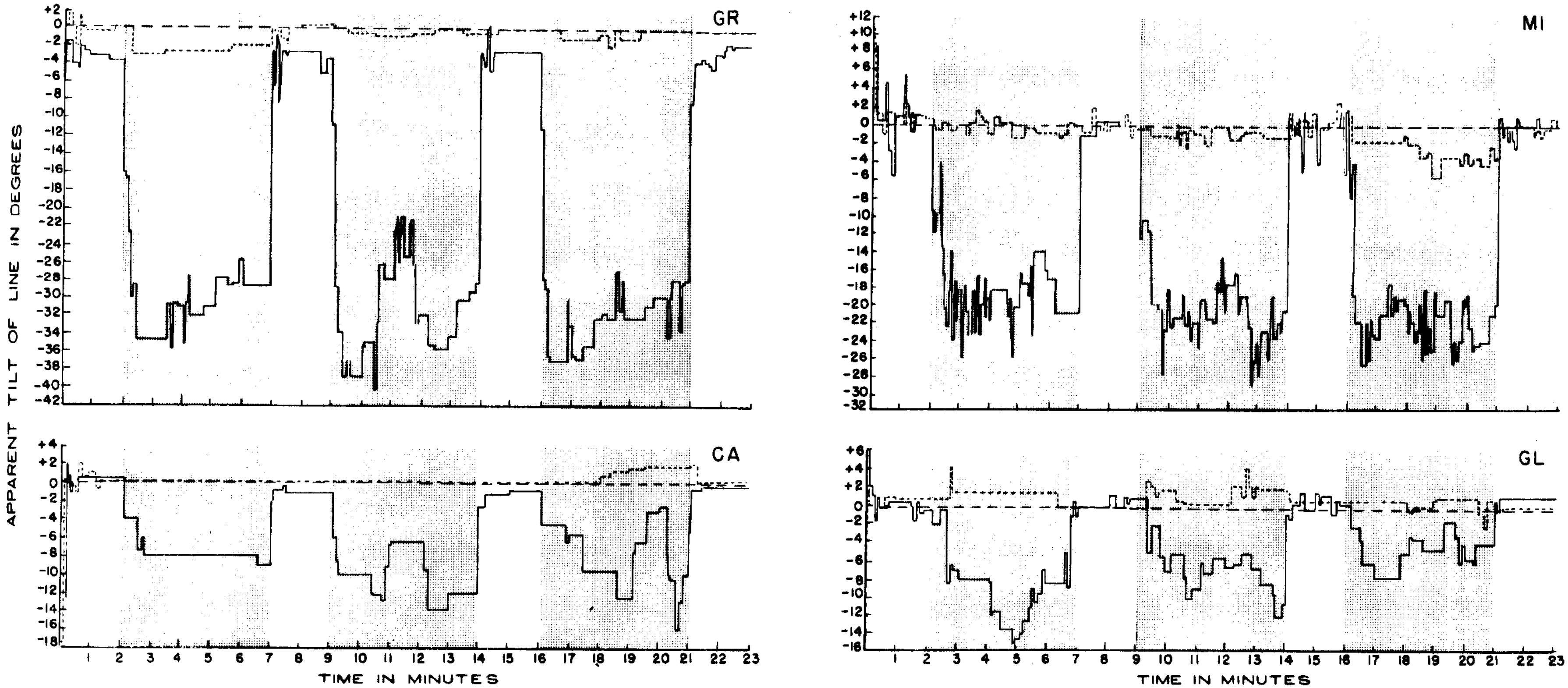
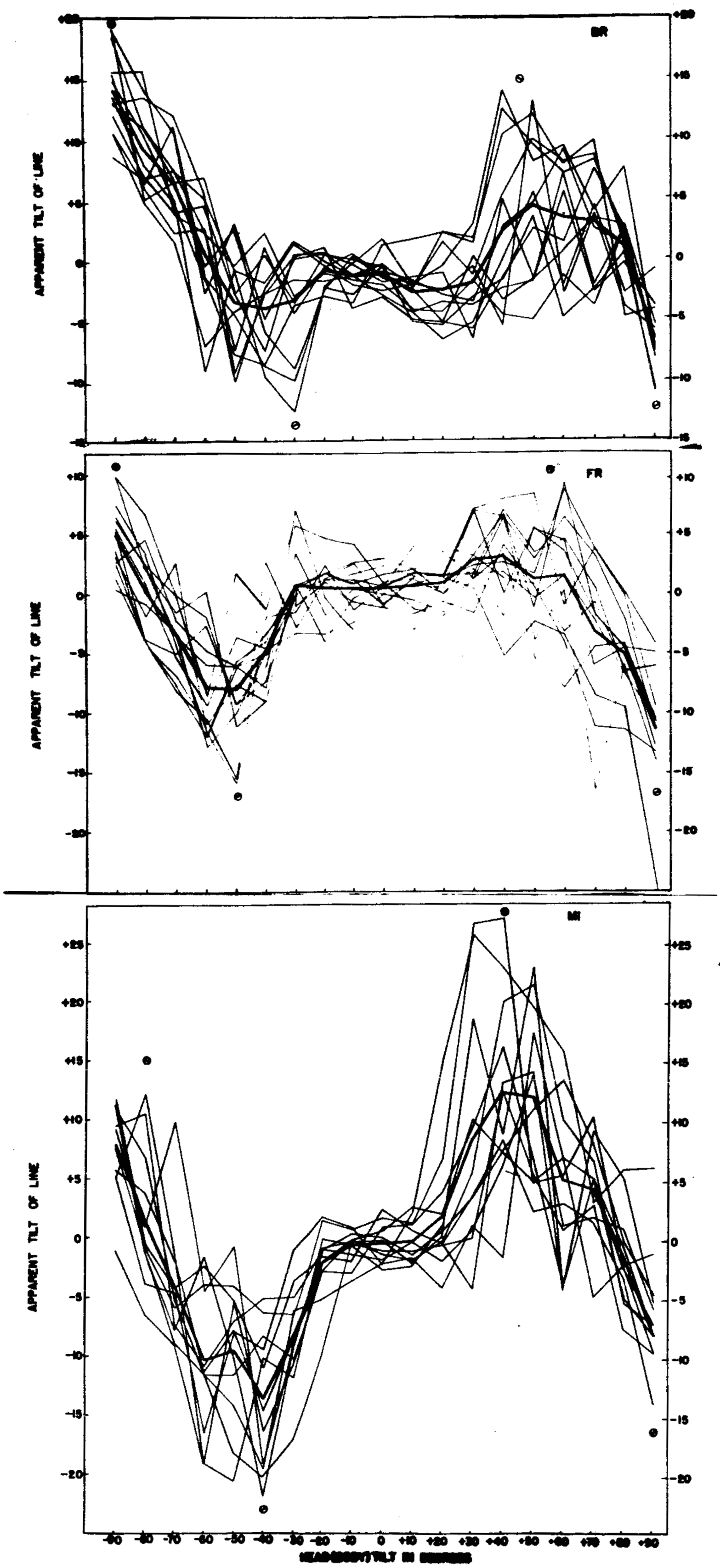

GR
MI
CA
GL
APPARENT TILT OF LINE IN DEGREES
TIME IN MINUTES
TIME IN MINUTES

Figure 6

Apparent Position of the Visual Horizontal as a Function of Head (Body) Tilt in Degrees as Tested in Three Subjects during each of Several Sessions. (Heavy Lines represents the Average of the Individual Session Curves [Thin Lines]).



BR
FR
MI
APPARENT TILT OF LINE
HEAD(BODY)TILT IN DEGREES

The variance in magnitude of deviation, however, does not appear to occur in a random manner but shows a regular dependence upon the position of the head (body). It is therefore possible to describe a characteristic qualitative pattern of response even though there are quantitative intertrial differences. In the three subjects tested at ten-degree intervals throughout the range of head tilts within $\pm 90^{\circ}$ from upright, the apparent visual horizontal tended to rotate in the same direction (E-phenomenon) as head (body) tilt in moderate amounts from upright, reaching a peak bilaterally at approximately 40 to 50 degrees. Then it reversed direction, causing the magnitude of deviation to decrease until the subjective was coincident with the objective horizontal. Tilting of the head beyond this point resulted in further displacement in the direction counter to head inclination (A- phenomenon). In all cases the deviation in the Aubert direction continued to increase on the average in proportion to head inclination beyond the "neutral" point so that the greatest deviation occurred at the maximum positions ($\pm 90^{\circ}$) of tilt used in this study.

Considerable information about these curious illusions has appeared in the literature since Aubert's original work, but quantitative data are scarce, especially in larger angles of head tilt. The underlying mechanisms are still not completely known. Counterrolling, a plausible explanation of the E-phenomenon involving the visual system only, has been cited by certain authors. If this be the sole or primary cause of this phenomenon, L-D subjects without this compensatory eye movement would be expected to manifest little or no E-phenomenon. A recent study (7) provides quantitative proof that this theory is untenable. A group of L-D subjects compared to a similar group of normals revealed significantly more deviation in the E direction in certain moderate angles of tilt.

An experiment (8) was also conducted in which a group of subjects with known bilateral labyrinthine defects was compared with a group of normal persons with respect to ability to judge horizontality as a function of upright, recumbent, and inverted posture. The fact that the Aubert illusion and its variants have been reportedly observed by certain deaf subjects by no means proves that the labyrinths do not influence this perception. On the contrary, although similar qualitative responses were found among all subjects, there were significant quantitative intergroup differences. When upright, the normals were able on the average to maintain their accuracy while the L-D subjects deviated significantly in their settings to the apparent visual horizontal when empirical visual cues were removed. Both groups of subjects in the recumbent position perceived the Aubert illusion, but the magnitude of the illusion was considerably less in the normal group. When inverted, both groups were less accurate in their estimates in the dark, but no significant intergroup difference was found.

In spite of the fact that there was some overlap in the group distributions of settings obtained in the upright and recumbent positions, indicating extra-labyrinthine factors were involved, the intergroup perceptual differences are best explained as an effect of the loss of vestibular function in the L-D subjects. It was concluded that the otolith organs in man act to increase his accuracy in egocentric visual localization at least in the upright and recumbent positions. This conclusion is in alignment with an earlier finding (9) in which a group of L-D subjects as compared to a group of normals perceived significantly greater amounts of autokinesis, another indicator of egocentric visual localization.

b. Oculogravic Illusion

1. Normal Subjects

Man seated upright can in effect be tilted by generating, as in the human centrifuge, a centrifugal force which is vectorially added to the standard gravitational force; as a result, upright is perceived in the direction of the resultant gravitational-inertial force. Tilting the subject with respect to gravity differs in one important aspect from tilting the gravitational-inertial resultant force with respect to the subject. The magnitude of the resultant force is always larger in the latter situation and bears a fixed but nonlinear relation to the angle phi.

It has long been known that normal persons perceive the oculogravic illusion, and some of its characteristics have been systematically investigated (10). Recent evidence (11) would indicate that the oculogravic illusion, as was found for the Aubert illusion, is a function of a number of complex factors other than input from the otolith organs. For example, this illusion increases with a reduction in visual framework exposed prior to the rendering of a judgment of horizontality. In making this judgment, however, using the frame of reference there was no evidence of adaptation in subjects exposed to constant centripetal force for four hours.

Normal subjects have been found to judge the visual horizontal in a similar manner which is more or less in accord with the resultant force environment (10). The curve (Figure 7) depicting the mean values obtained by discrete settings to the apparent horizontal is typical of normal subjects. When continuous adjustments of the visual horizontal are made, a long delay is regularly observed between the time of peak acceleration and the time of the subject's peak response. This is perhaps due in part to a response lag of the peripheral sense organ, but is thought to be primarily due to delay in central nervous system mechanisms. A delay of similar character was seen in the static tilt studies.

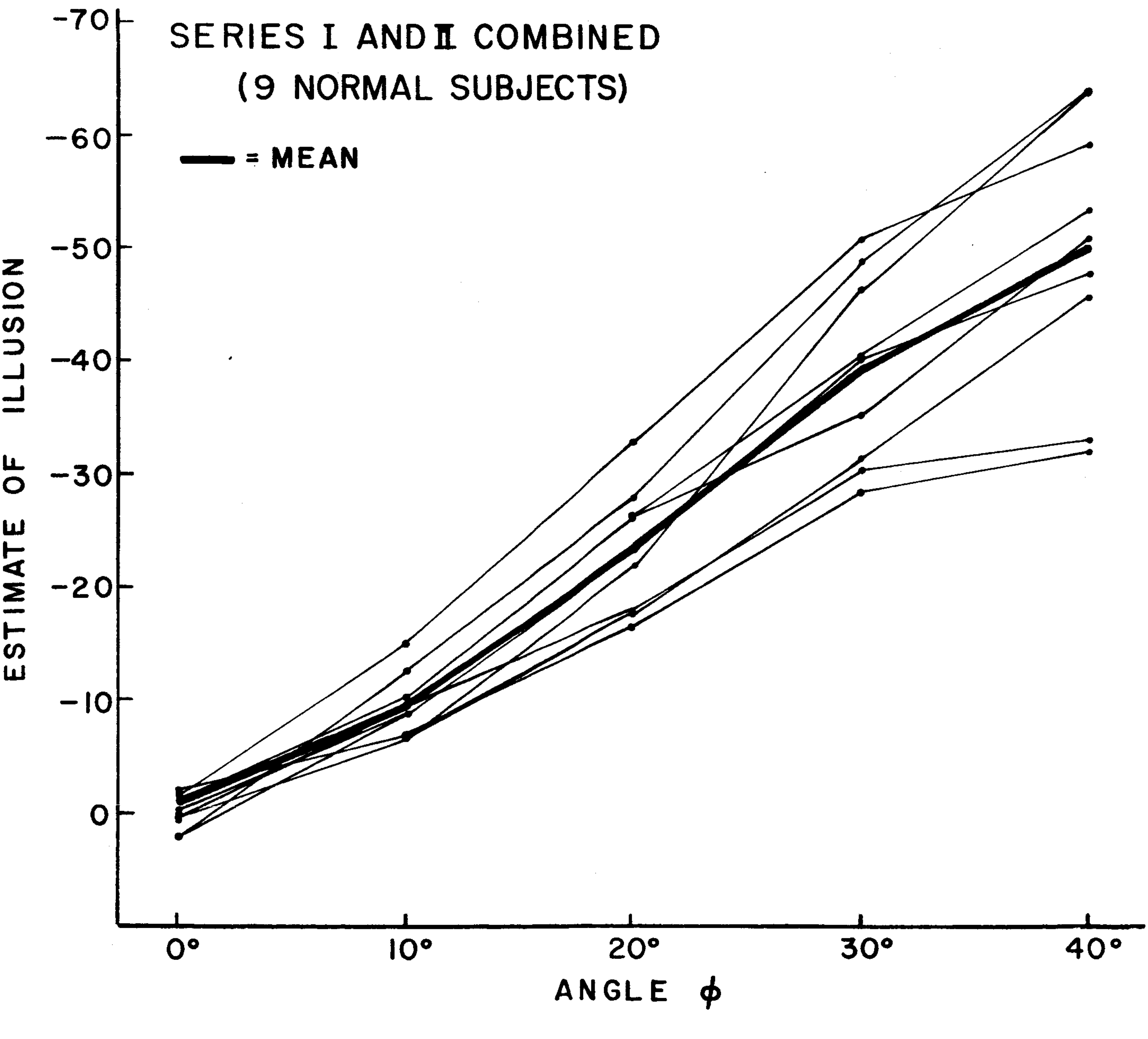
2. <u>Labyrinthine Defective Subjects</u>

Failure to perceive the oculogravic illusion has been ascribed to loss of function of the otolith apparatus, but few studies had been carried out on L-D subjects and few quantitative data were available

Figure 7

Estimates of OGI by Normal Subjects. Single Settings of Luminous Line.

(Graybiel and Clark, Aerospace Med.)

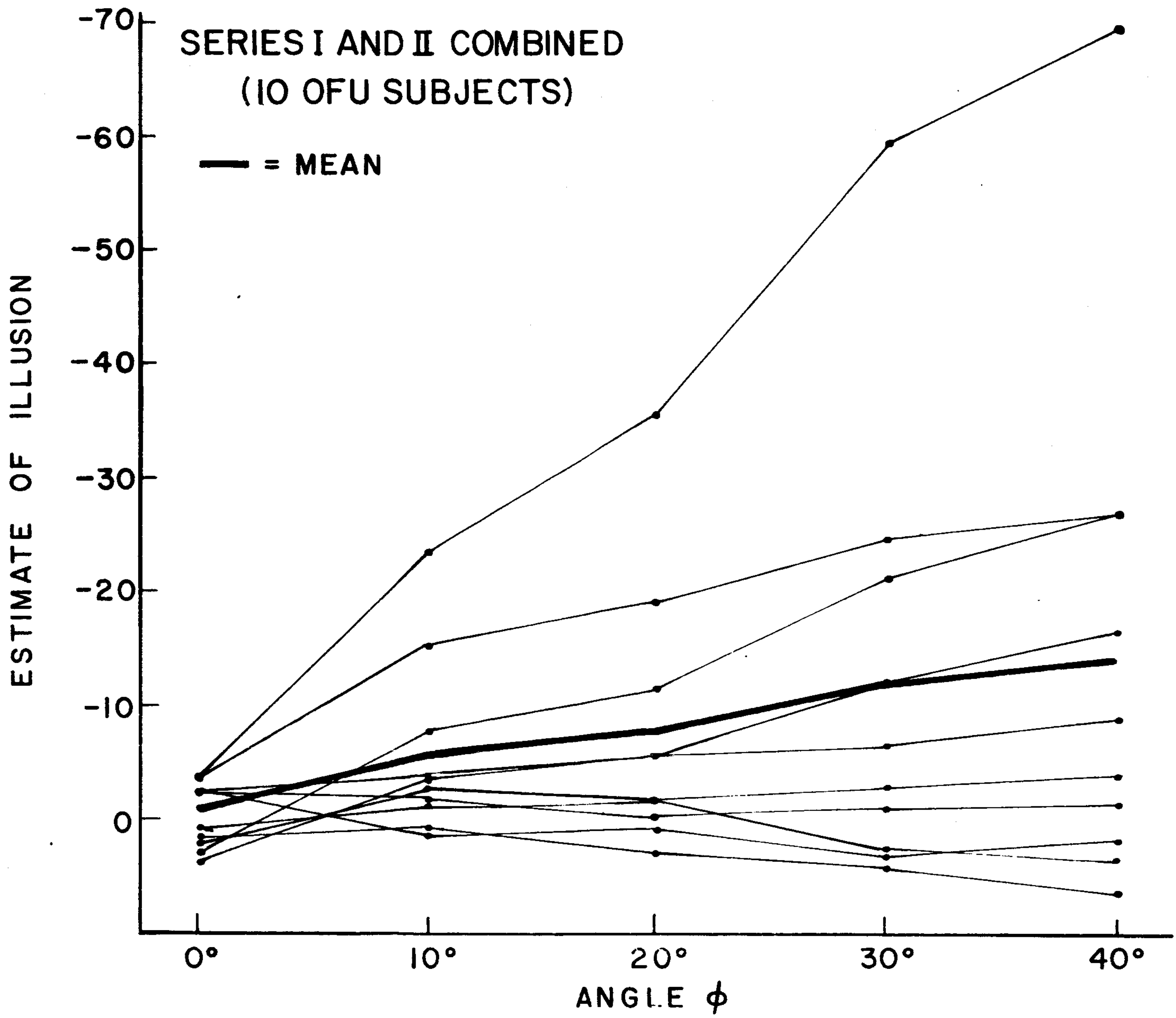


SERIES I AND II COMBINED
(9 NORMAL SUBJECTS)
= MEAN
ESTIMATE OF ILLUSION
-70
-60
-50
-40
-30
-20
-10
0
0°
10°
20°
30°
40°
ANGLE ϕ

to validate this claim. A study (12) was therefore conducted to determine the validity of the oculogravic illusion as a specific indicator of otolith function. A group of deaf subjects having complete functional loss of their semicircular canals but with unknown functional loss of the otolith organ was compared with a group of normal subjects in regard to the oculogravic illusion. In selecting naturally occurring experimental subjects with labyrinthine defects, the usual procedure is to screen a group of deaf persons, selecting those who also have lost the function of the semicircular canals. In doing this, it was not assumed that loss of all canal function was a valid indication of the complete loss of otolith function. Indeed, evidence from counterrolling and the study just cited indicates that this assumption may be erroneous in some cases. The mean discrete settings to the apparent horizontal of the L-D subjects, in contrast to the normal group, were not characteristic for all members of the group (Figure 8). Indeed, the variability was so great that consideration of the results of individual subjects in this group was necessary. Differences among subjects in the L-D group are explicable on the assumption that in certain members there was a specific level of residual function of the otoliths and in others it was lost completely. Unilateral labyrinthine loss does not abolish the illusion (13).

Figure 8

Estimates of OGI by Labyrinthine Defective Subjects. Single Settings of Luminous Line. (Graybiel and Clark, Aerospace Med.)


SERIES I AND II COMBINED
(10 OFU SUBJECTS)
= MEAN
-70
-60
-50
-40
-30
-20
-10
0
ESTIMATE OF ILLUSION
0°
10°
20°
30°
40°
ANGLE ϕ

SEMICIRCULAR CANALS AND VISION

Nystagmus, induced by thermal stimulation or in response to angular or Coriolis acceleration, serves as an indicator of semicircular canal function but its use in this regard is complicated by factors which may alter or abolish it. For example, it can be increased by mental activity. On the other hand, it can be reduced by introducing a visual fixation field or by requiring a subject to repeat a particular pattern of vestibular stimulation. The reduction in nystagmic response through stimulus repetition may stem from a loss of arousal or drowsiness, but there is also evidence to show that nystagmus may be actively suppressed. Restriction of head movements to certain patterns diminished nystagmus during a 64-hour exposure to rotation at 5.4 RPM within a 15-foot diameter rotating room (13). Efforts to maintain alertness by instructions did not restore nystagmus. Moreover, the nystagmus measured following the rotational period was opposite in direction to the response produced by the same head movement during rotation indicating that it was a conditioned response in as much as the stimulus was no longer Coriolis acceleration. Similar evidence of habituation was obtained from the subjective reports of the apparent motion (oculogyral illusion) of a target light in an otherwise dark room. For conditioning purposes, head movement was confined to one quadrant of the frontal plane. Subsequent tests were then made in this quadrant (practiced) and the opposite quadrant (unpracticed). Dramatic reductions in response occurred in the practiced quadrant but habituation was not transferred to the unpracticed quadrant (Figure 9).

VESTIBULAR ORGAN INTERACTION AND VISION

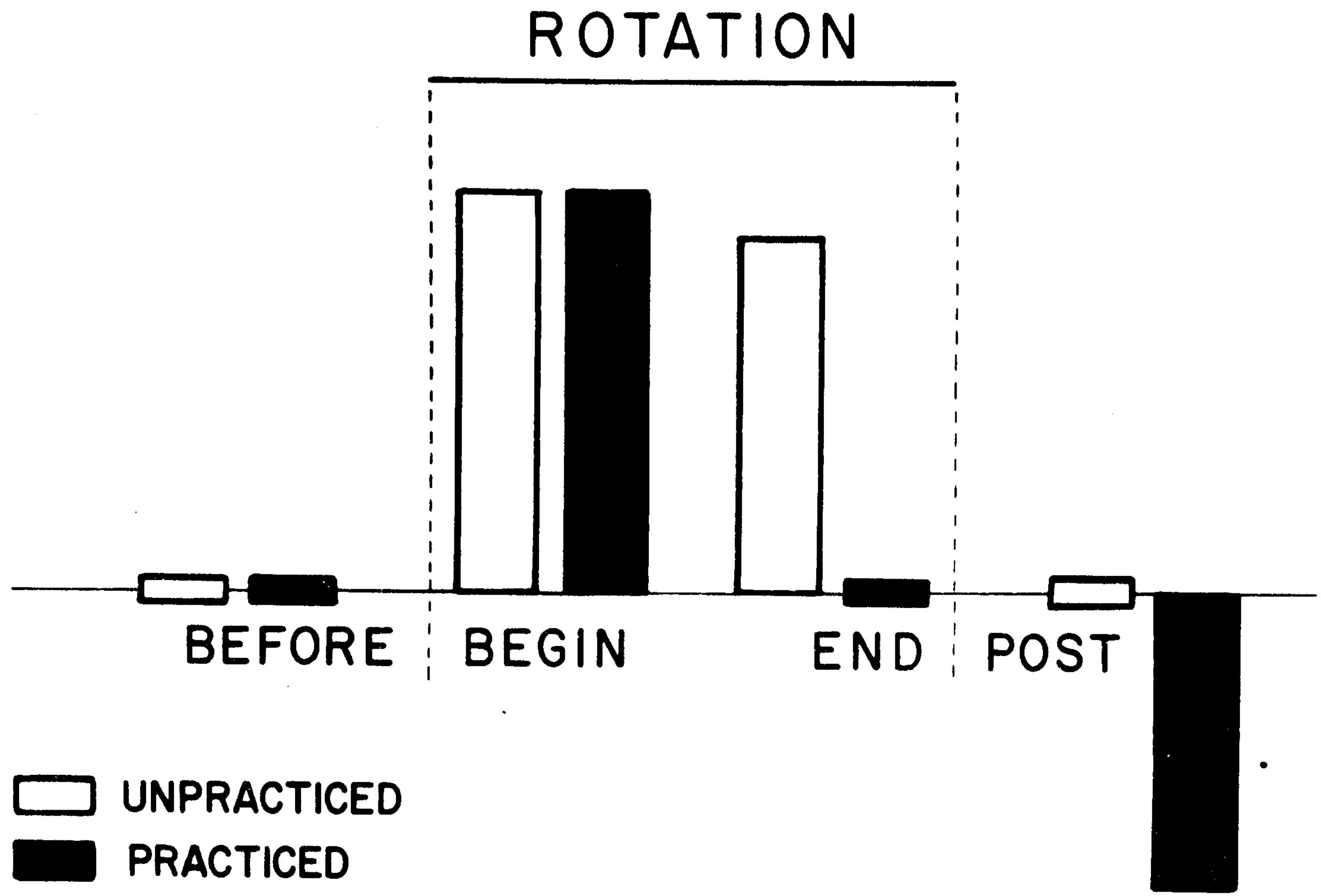
It is obvious that, in many areas, research concerning the interaction between vision and the vestibular organs has only begun. Differentiating the function of the otolith and cupula organs has occupied the interest of many investigators in the past, but the complete understanding of vestibular organs and their combined influence upon vision.

Based upon overwhelming evidence, there can be little doubt that the so-called vestibular nystagmus is released by the action of the semicircular canals and, as in the examples cited above, is modified by the CNS. A basic question that now needs to be answered is whether under special circumstances the otolith organ may also either release independently or contribute an essential element for its release by the canals. The fact that nystagmus can be elicited in certain individuals by simply changing the position of the head is strong evidence that the otolith organ is involved in this ocular response.

Figure 9

Comparative Magnitude and Direction of the Coriolis Illusion Associated with Single Head Movements Before, During and After Prolonged Rotation at 5.4RPM. Tests Carried out at 7.5 RPM. (Graybiel, Ashton, Vestibular Sickness and Some of Its Implications for Space Flight. Neurological Aspects of Auditory and Vestibular Disorders. Courtesy of Charles C. Thomas, Publisher, Springfield, Illinois.).

COMPARATIVE MAGNITUDE AND DIRECTION OF THE CORIOLIS ILLUSION ASSOCIATED WITH SINGLE HEAD MOVEMENTS BEFORE, DURING AND AFTER PROLONGED ROTATION AT 5.4 RPM. TESTS CARRIED OUT AT 7.5 RPM.



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